# MORPHOLOGY AND PHYLOGENETIC SIGNIFICANCE OF THE CORNERS AND MIDLINES OF THE CONULARIID TEST

by HEYO VAN ITEN

ABSTRACT. The hypothesis that conulariids were closely related to scyphozoan cnidarians is based in large part on interpretations of the morphology of the corners and midlines of the conulariid test. Corners and/or midlines of some or all species of at least ten of the twenty-one currently recognized conulariid genera are internally thickened. Internal midline structures of some or all species of six genera are paired or adaxially bifid. Midlines of one species, *Eoconularia amoena* Sinclair, exhibit features suggesting the presence of a single carina that bifurcates adaperturally. Species of five genera exhibit internal structures both at the corners and the midlines. In almost all of these taxa, internal structures at the corners are broader and/or higher than associated midline structures. Internal corner and/or midline structures of some members of two genera are seriated. Conulariid corners and midlines show a number of similarities to soft-part and thecal structures located, respectively, at the scyphozoan perradii and interradii. Nearly all of these similarities are uniquely shared by conulariids and scyphozoans, and corroborate Kiderlen's (1937) hypothesis that conulariid midlines were sites of a gastric septum, homologous to the gastric septa of scyphozoans.

MUCH of the controversy surrounding the analysis of conulariid affinities can be traced to conflicting interpretations of the corners and midlines of the steeply pyramidal, finely lamellar conulariid test. Corners and/or midlines of many conulariids are sites of localized inflection and thickening of the test's inner lamellae (e.g. Wiman 1895; Knod 1908; Reed 1933; Bouček 1939; Van Iten 1991). Based on comparisons of internal conulariid test structures with soft-part and internal thecal structures of scyphozoan cnidarians, conulariid midlines have been interpreted as former sites of a gastric septum, homologous to the gastric septa of scyphozoans (e.g. Kiderlen 1937; Moore and Harrington 1956; Werner 1966*a*, 1966*b*, 1967; Bischoff 1978; Möhn 1984; Van Iten 1991). Scyphozoan septa are normally four in number and lie within one of two mutually perpendicular planes of symmetry, called the interradii. Bisecting the angles between the interradii are two additional symmetry planes, the perradii, that intersect the corners of the rectangular scyphozoan mouth. Conulariid corners, usually situated along two planes that lie more or less midway between two planes containing the midlines, have been interpreted as comparable in position to the scyphozoan perradii. These anatomical relationships are illustrated in Text-figure 1.

This and other hypotheses of homology between conulariids and scyphozoan cnidarians have been questioned by a number of authors (Termier and Termier 1949, 1953; Kozlowski 1968; Oliver 1984; Steul 1984; Mortin 1985; Feldmann and Babcock 1986; Babcock and Feldmann 1986*a*, 1986*b*; Oliver and Coates 1987; Babcock 1991; Yochelson 1991). Yet none of these authors has proposed that conulariid corners and midlines are more similar (and therefore more likely to be homologous) to test or soft-part structures of non-scyphozoan groups. Instead, rejection of the hypothesis that conulariid midlines were sites of a gastric septum has generally been based on claims that (1) conulariids and scyphozoans exhibit fundamental dissimilarities (Termier and Termier 1949, 1953; Kozłowski 1968; Steul 1984; Mortin 1985; Feldmann and Babcock 1986; Babcock and Feldmann 1986*a*, 1986*b*; Babcock 1991; Yochelson 1991); and that (2) similarities between conulariid corners and midlines and features at the scyphozoan perradii and interradii are superficial (Termier and Termier 1949, 1953; Kozłowski 1968; Oliver 1984; Feldmann and Babcock
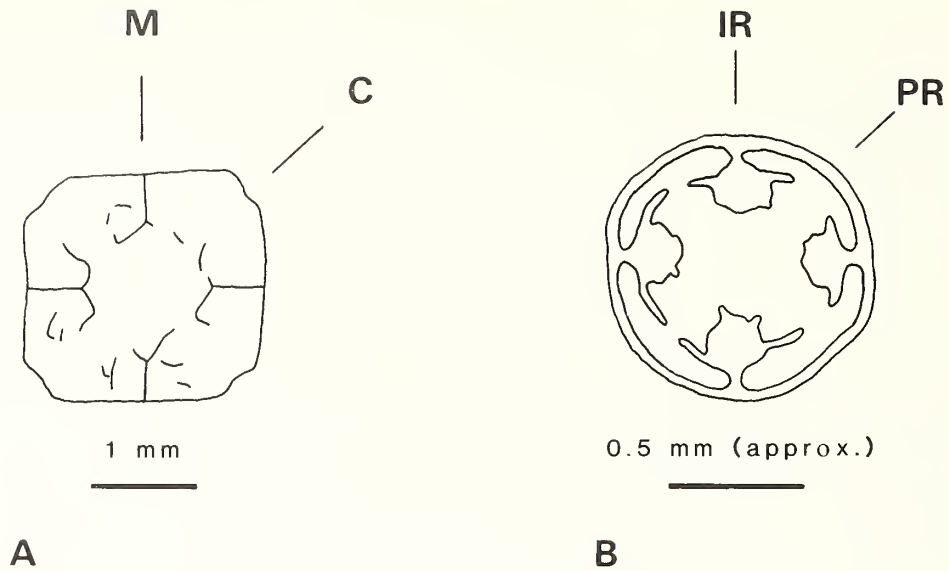
TEXT-FIG. 1. Transverse cross sections through A, the conulariid *Eoconularia loculata* (Wiman); B, *Craterolophus tethys* Clarke, a stauromedusan scyphozoan. Letter symbols are as follows: M, midline; C, corner; IR, interradius; PR, perradius. Text-fig. 1A taken from Wiman (1895, pl. 5, fig. 11); Text-fig. 1B taken from Kiderlen (1937, fig. 31), with information on scale taken from Gross (1900, pl. 23).

1986; Babcock and Feldmann 1986*a*, 1986*b*; Oliver and Coates 1987; Babcock 1991; Yochelson 1991).

The present analysis of conulariid corners and midlines is based in part on new information on the anatomy and occurrence of internal test structures at these sites. In order better to organize our knowledge of this critical aspect of conulariid anatomy, new data on corners and midlines are presented in the context of a general survey of conulariid cross-sectional geometry and internal anatomy. Several previous investigators have also contributed to our knowledge of conulariid corner and midline anatomy. Among the most important earlier studies are Wiman's (1895) paper on *Eoconularia loculata* (Wiman), Sinclair's (1940) paper on *Metaconularia* Foerste, and Bischoff's (1978) paper on circoconulariids, a group of steeply conical (as opposed to steeply pyramidal)

EXPLANATION OF PLATE 1

Examples of conditions of conulariid corner and midline anatomy recognized in the present study (all photos taken with SEM, figure 2 in backscattered electron mode).

Fig. 1. *Simple groove* (SG); inner surface of part of a corner of *Conularia trentonensis* Hall; UMMP 66013; Middle Ordovician; New York, × 25.

Fig. 2. *Carinate groove* (CG); transverse section through a corner of *Climacoconus* sp.; SUI 61531; Upper Ordovician; Iowa, × 80.

Fig. 3. Fragmentary corner of another *Climacoconus* specimen exhibiting two ridges (arrows) interpreted here as parts of a seriated carina; GSC 94786*a*; Middle Ordovician; Minnesota, × 20.

Fig. 4. *Simple midline* (S); inner surface of part of a midline of *Conularia trentonensis* Hall; UMMP 66013; Middle Ordovician; New York, × 25.

Fig. 5. *Single carina* (SG); inner surface of part of a midline of *Conularia splendida* Billings; the midline carina of this species is often bifid (see text and Pl. 2, fig. 6); UMMP 66123; Upper Ordovician; Iowa, × 23.

Fig. 6. *Paired seriated carinae* (PSC); inner surface of part of one face of an undetermined species of *Climacoconus*, showing pairs of I-shaped ridges flanking the midline; ridges to the right of the midline have been broken and displaced from their original positions; GSC 94785*a*; Upper Ordovician; Iowa, × 30.

PLATE 1

VAN ITEN, *Conularia, Climacoconus*
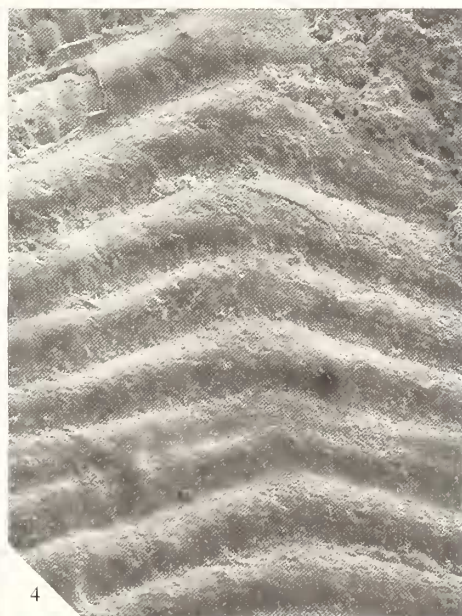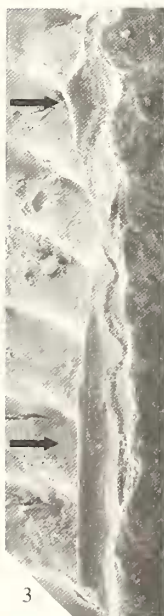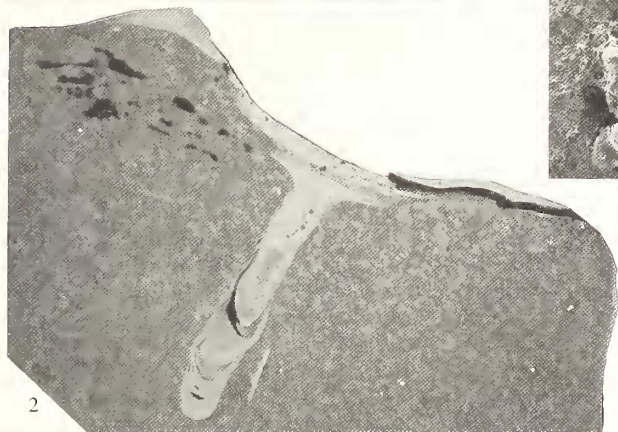
Problematica interpreted by Bischoff (1978) as a taxon within Conulariida. Together with information gathered by previous investigators, results of this study reveal that conulariid corners and midlines are more complex anatomically than has hitherto been realized. Now that our knowledge of conulariid corner and midline anatomy is more complete, we are in a better position to evaluate whether or not similarities between conulariids and scyphozoans are indicative of a close phylogenetic relationship.

MATERIAL AND METHODS

The present study is based on examination of some or all known species of fourteen of the twenty-one currently recognized conulariid genera, supplemented by data presented in previous papers (Barrande 1867; Ulrich 1892; Holm 1893; Wiman 1895; Slater 1907; Knod 1908; Bouček 1928, 1939; Sinclair 1940, 1941, 1942, 1944, 1948; Sugiyama 1942; Bischoff 1978) on members of these and two other genera. Specimens from the following genera were studied: *Anaconularia* Sinclair, *Archaeoconularia* Bouček, *Calloconularia* Sinclair, *Climacoconus* Sinclair, *Conularia* Miller, *Conularina* Sinclair, *Ctenoconularia* Sinclair, *Eoconularia* Sinclair, *Glyptoconularia* Sinclair, *Metaconularia* Foerste, *Notoconularia* Thomas, *Paraconularia* Sinclair, *Pseudoconularia* Bouček, and *Reticulaconularia* Babcock and Feldmann. Information on the identity, location, and age and host horizon(s) of these specimens is presented in the Appendix. Also presented in the Appendix are explanations of repository abbreviations used in the text. Availability of specimens varies widely from genus to genus, with some genera (e.g. *Ctenoconularia* and *Eoconularia*) known only from a handful of specimens, mostly non-preparable types, and others (e.g. *Conularia* and *Paraconularia*) represented by hundreds or even thousands of specimens. Fortunately, type specimens of some of the rare taxa are often broken or exfoliated in such a way as to permit inspection of the test's inner surface.

Depending on the nature of the host matrix, specimens were prepared in one of two ways. Specimens embedded in acid resistant, non-calcareous matrix were sectioned. Sections were cut perpendicular to the specimen's long axis, or parallel to it, along a pair of opposite corners or midlines. Other specimens, preserved in limestone, were embedded in casting resin and then cut in half longitudinally. The two halves were immersed in 10 per cent formic acid until the internal matrix was dissolved, thus revealing the test's inner surface. Wherever possible, specimens were chosen that preserved or were broken near the apertural margin and that tapered to within a few millimetres or less of the apex.

CONULARIID CORNERS AND MIDLINES

Conditions of conulariid corners

Non-sulcate (NS). Corners of a small number of conulariids appear to have been characterized by the absence of a sulcus or groove. This condition was originally detected in *Anaconularia*, a monospecific genus currently known only from sandstone steinkerns (Barrande 1867; Bouček 1928; Sinclair 1948, 1952). As indicated by present observations and those of previous studies, the corners of all of the 2000 or so steinkerns collected thus far are rounded and show no evidence of a groove or internal test thickening. According to Sugiyama (1942), non-sulcate corners also characterize *Conulariopsis* Sugiyama, a monospecific genus from the Lower Triassic of Japan.

Simple groove (SG) (Pl. 1, fig. 1). Except in the two taxa just mentioned, corners of all conulariids are furrowed by a broad sulcus or groove. In many taxa, this groove is not accompanied by internal test thickening. As indicated by present observations and those of previous studies (Barrande 1867; Bouček 1928; Sinclair 1940, 1941, 1948), this condition characterizes most (and possibly all) currently recognized species of *Metaconularia* and *Pseudoconularia*, and most species of *Conularia*. It also characterizes some species of *Climacoconus*, *Ctenoconularia*, and *Paraconularia* (see Appendix).

Mesially folded groove (MFG). This condition constitutes the sole diagnostic feature of *Notoconularia*, erected by Thomas (1969) to receive three Permo-Triassic species formerly assigned to *Paraconularia*. Although apparently not accompanied by internal test thickening, corner grooves of *Notoconularia* differ from simple grooves in exhibiting an outwardly directed, mesial fold.

TEXT-FIG. 2. Line drawings of longitudinal profiles of three seriated corner carinae in a specimen of an undetermined species of *Climacoconus* from the Elgin Member of the Maquoketa Formation (Upper Ordovician); northeast Iowa, USA; SUI 61534. The midlines of this specimen lack internal structures.

Aperture

5 mm
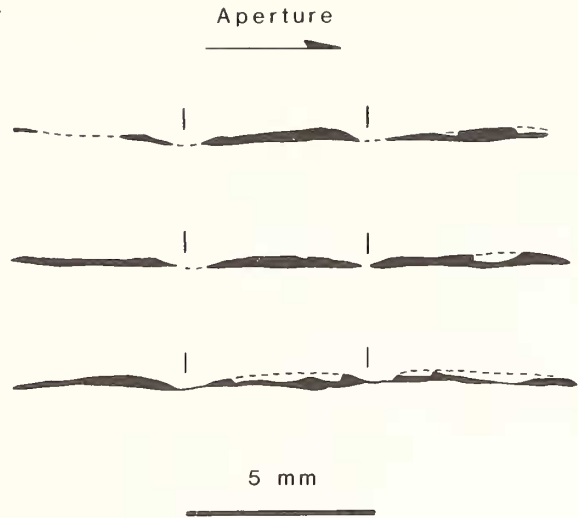
Carinate groove (CG) (Pl. 1, figs 2–3). Corners of a large number of sulcate conulariids exhibit a broadly rounded or keel-like internal carina. This condition characterizes some or all species of *Archaeoconularia*, *Calloconularia*, *Climacoconus*, *Conularia*, *Conularina*, *Ctenoconularia*, *Eoconularia*, *Glyptoconularia*, and *Paraconularia* (see Appendix). Corner carinae here observed are generally more or less continuous and, in many specimens, strongly pigmented. In nearly all taxa they are very prominent (e.g. Text-fig. 3), with carinae of some *Climacoconus* specimens (e.g. UMMP 20560*a*) locally extending up to about one-third of the distance to the centre of the test cavity.

Evidence of seriation was observed in corner carinae of two specimens of *Climacoconus*. Three carinae in one of these specimens (the fourth carina is not preserved), collected from the Maquoketa Formation (Upper Ordovician) of northeast Iowa, USA, consist of three elongate segments (Text-fig. 2). The segments range from approximately 4–5 mm long and exhibit a gently arcuate longitudinal profile (locally disrupted by breaks sustained during preparation). Consecutive segments along the same carina are separated by a short stretch of non-carinate test, and isolatitudinal segments on different carinae begin and end at approximately the same distance from the apex.

The second specimen (Pl. 1, fig. 3), collected from the Platteville Formation (Middle Ordovician) of southeast Minnesota, USA, preserves portions of two segments of a single carina. This specimen is one of several Platteville *Climacoconus* specimens assigned by Sinclair (1948) to *C. concinnus*, a species that was never published. Although the geometry of the corner carina in other *C. concinnus* specimens could not be determined (due to incomplete preservation and scarcity of available material), midlines of this species are straddled by a pair of seriated carinae, described below.

The arcuate geometry of the ridges described above indicates that they are not the result of breakage or incomplete preservation. The two specimens displaying these ridges show no signs of injury or malformation; their transverse ornament is normal, and their corners diverge more or less continuously, with no apparent constriction at the ends of carina segments. These observations suggest that the carina anatomy displayed by these specimens is not accidental, but a type of seriation.

Conditions of conulariid midlines

Simple (S) (Pl. 1, fig. 4). Midlines of many conulariids are furrowed by a groove and/or exhibit one or two internal thickenings or carinae. Midlines that lack these features are referred to here as simple. Simple midlines characterize species of *Conularia*, *Climacoconus*, *Ctenoconularia*, *Noto-*

conularia, *Paraconularia*, and *Reticulaconularia*. Simple midlines apparently also characterize *Conulariella* Bouček (see for example Bouček 1939, fig. 10).

Outwardly folded (OF). This condition is diagnostic of the genus *Pseudoconularia* (Bouček 1939; Sinclair 1941, 1948). In this taxon, each midline is marked by a low, broad, outwardly-projecting longitudinal fold. As indicated by inspection of figures in Barrande (1867, pls 3–7) and exfoliated areas on the holotype of the only known North American species of this genus (Sinclair 1941; see also Appendix), portions of the test comprised by the fold are non-thickened.

Single carina (SC) (Pl. 1, fig. 5). Midlines of a number of conulariids are sites of a single, broadly rounded or keel-like internal carina. This condition characterizes some or all species of *Archaeoconularia*, *Calloconularia*, *Climacoconus*, *Conularia*, *Eoconularia*, and *Paraconularia* (see Appendix).

In addition to having carinate midlines, the North American species *Eoconularia forensis* Sinclair and *Paraconularia crustula* (White), and the European species *Archaeoconularia fecunda* (Barrande), also possess carinate corners. In *E. forensis*, currently represented by three known specimens (see Appendix), the corner carinae are about four times higher and three times wider than the midline carinae (Text-fig. 3A). Judging from illustrations in Barrande (1867, pl. 8, fig. 9) and Bouček (1939, fig. 2a; Text-fig. 3B herein), the corner carinae of *A. fecunda* are likewise higher and broader than the midline carinae. In *P. crustula*, corner carinae of eight of 18 specimens here examined (see Appendix) are distinctly higher than the midline carinae (Text-fig. 3C), while in the remaining specimens the two sets of carinae are about equally high. (Internal thickening at both corners and midlines was also observed in *Calloconularia strimplei* Sinclair (Pennsylvanian, USA; see Appendix), but due to restrictions on sample preparation the relative sizes of the two sets of internal test structures could not be determined.)

Ulrich (1892, pl. 3, fig. 6a) and Knod (1908, pl. 24, figs 1–2, pl. 31, fig. 3; see also Moore and Harrington 1956, fig. 26) documented a prominent carina at corners and midlines of two specimens collected from the Devonian of Brazil and later identified by Babcock *et al.* (1987b) as *Conularia albertensis* Reed. Babcock *et al.* (1987a, fig. 10B) figured a carinate specimen of the same species from the Devonian of South Africa. In this specimen and the one figured by Ulrich (1892), the carina at the corners is distinctly larger than the carina at the midlines.

Groove with seriated carina (GSC) (Pl. 2, fig. 1). Midlines of *Archaeoconularia* are furrowed by a distinct sulcus (Bouček 1939; Sinclair 1944, 1948), and a very weak groove apparently marks the midlines of *Glyptoconularia*. In the North American species *A. membranacea* (Ringueberg), currently represented by two incomplete specimens (see Appendix), the midlines are also sites of internal thickening. Viewed internally, preserved portions of two midlines of the holotype and most complete specimen (the inner surface of the other two midlines of this specimen cannot be seen) exhibit a series of extremely low, narrow, closely-spaced ridges, running along the crest of the midline groove. The ridges range from approximately 0·4 to 0·8 mm long and are about 0·05 mm wide. They may be more or less contiguous or spaced up to about 0·8 mm apart. Each ridge exhibits a gently arcuate longitudinal profile, with a maximum height near the centre of the ridge of approximately 0·05 mm. Similar ridges occur on portions of two midlines of a fragmentary specimen (BMS 10793) from the same locality.

The geometry of these ridges indicates that they are not artifacts of breakage or incomplete preservation, and the specimens themselves show no sign of injury or malformation. Thus the ridges are probably best interpreted as members of a low, seriated carina.

The corners of *A. membranacea* are sites of a continuous (non-seriated) carina. This structure is substantially higher and broader than the seriated midline carina.

Paired carinae (PC) (Pl. 2, figs 2–4). This condition, previously detected in *Metaconularia* (e.g. Holm 1893; Slater 1907; Sinclair 1940, 1948), apparently also characterizes at least one species each of
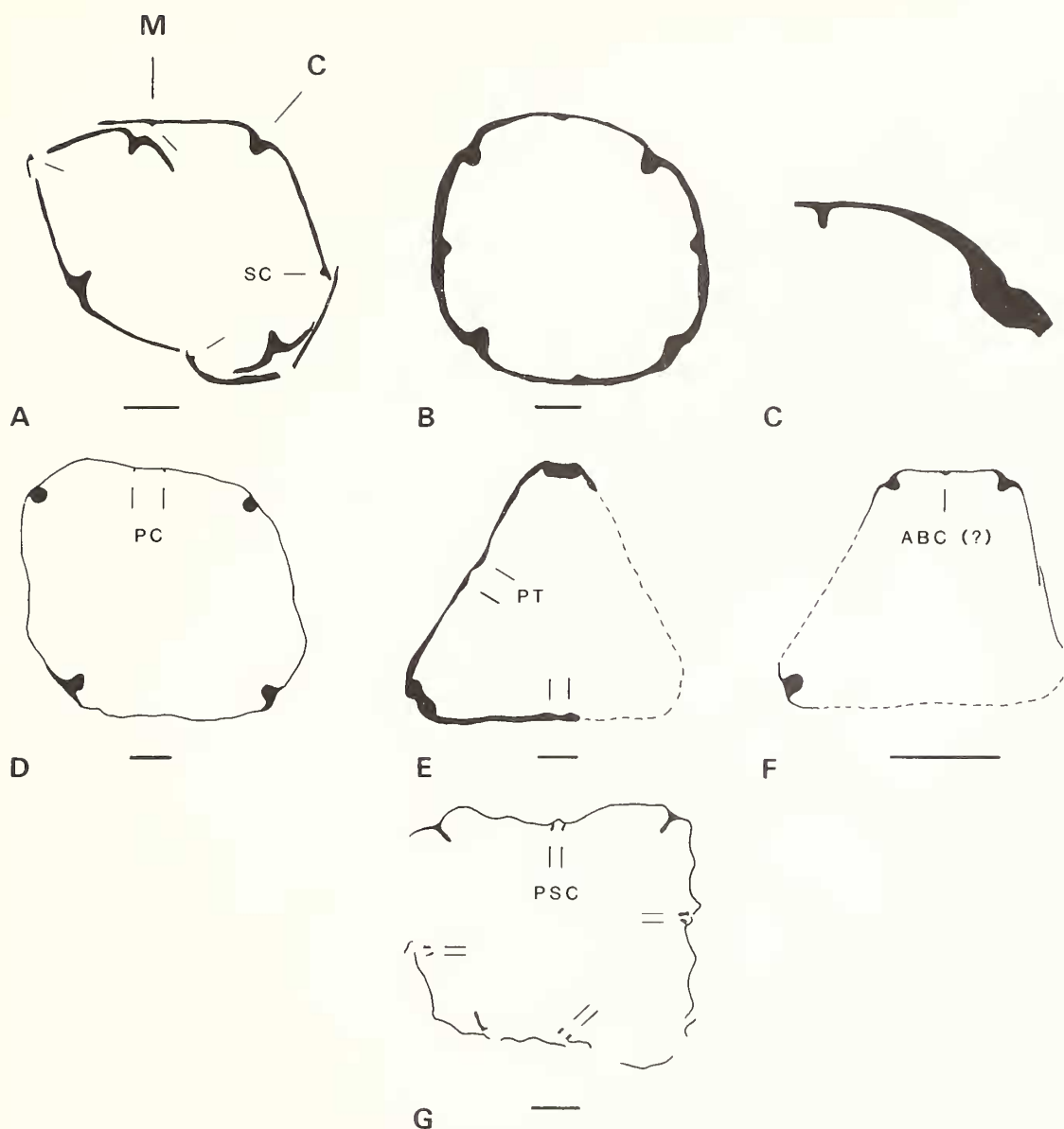
TEXT-FIG. 3. Line drawings of transverse sections through conulariids having internal structures at both corners (C) and midlines (M). All scale bars = 5 mm. A, *Eoconularia forensis* Sinclair; GSC 87201. B, *Paraconularia crustula* (White); UMMP 66024*b*. C, *Archaeoconularia fecunda* (Barrande) (modified from Boucek 1939, fig. 2*a*). D, *Conularina narrawayi* Sinclair; ROM 18905. E, *Conularina triangulata* (Raymond); GSC 94788. F, *Eoconularia amoena* Sinclair; ROM 23297. G, *Climacoconus* sp.; SUI 61531.

Conularina and *Paraconularia*. It is defined by a pair of low, broadly rounded or keel-like ridges, with members of each pair situated on opposite sides of the midline proper. Paired midline carinae of *Metaconularia* (Pl. 2, fig. 2) diverge towards the aperture, at approximately 1–2°, and project from about one-fiftieth to one-twentieth of the distance to the opposite midline. They are often strongly pigmented. Carinae of exceptionally complete specimens (e.g. specimens of *M. manni* (Roy)

and *M. aspersa* (Slater); see Appendix) extend nearly the entire length of the test and are discrete throughout their length. Such carinae show a very gradual, more or less continuous increase in height and width towards the aperture over most of their length.

As noted by Sinclair (1940), some species of *Metaconularia*, for example *M. papillata* (Hall) (Middle Ordovician, New York), exhibit a distinct groove along the midline proper. Observations presented in Barrande (1867, pl. 8, figs 17–18, 20–22) suggest that paired carinae flanking a grooved midline also characterize *Metaconularia? modesta* (Barrande).

Features interpreted here as fragments of paired midline carinae occur in *Conularina narrawayi* Sinclair, currently represented by a single incomplete specimen from Middle Ordovician strata in Quebec (Pl. 2, fig. 3). Paired midline carinae in this specimen are extremely low and narrow. The corners of this specimen are also carinate, but the corner carinae are about five times higher and eight times wider than those at the midlines (Text-fig. 3D).

Inspection of a photograph in Sinclair (1942, pl. 2, fig. 2) suggests that paired carinae also characterize midlines of *Conularina undosa* Sinclair, another species from the Middle Ordovician of Quebec. Unfortunately, the holotype and only described specimen of this species is now missing.

A pair of very low, apparently discontinuous carinae or thickenings were observed in specimens of *Paraconularia chesterensis* (Worthen), currently known from Lower Mississippian strata of the United States (Babcock and Feldmann 1986c). Midlines of two specimens (ISGS/ISM 2489 and UMMP 23955; Pl. 2, fig. 4), collected from lime grainstones in the Chesterian Series of Illinois, are discontinuously straddled by a pair of narrow, dark colour bands. Members of each pair of bands are spaced approximately 1 mm apart and diverge very gradually towards the aperture. As indicated by inspection of sectioned or exfoliated areas (e.g. Pl. 2, fig. 4), each band is associated with very low but distinct internal test thickening. Due to poor preservation or restrictions on preparation, it could not be determined whether midlines of other specimens of *P. chesterensis* exhibit paired tracts of longitudinal thickening like those described above. However, a number of specimens (e.g. specimens from the Edwardsville Member of the Muldraugh Formation of Indiana; LACM 9364) exhibit colour banding at the midlines, and one of these specimens (LACM 9364a) shows internal thickening on at least one side of its only preserved midline.

Paired thickenings (PT) (Pl. 2, fig. 5). This condition characterizes three of the five currently recognized North American species of *Conularina* Sinclair, including the unusual form *C. triangulata* (Raymond), which has three (rather than four) faces (Sinclair 1942, 1948). It consists of a pair of broad, very low, continuous thickenings, one on either side of the midline proper. Although similar to paired carinae, paired thickenings differ from the latter in being substantially

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EXPLANATION OF PLATE 2

Additional conditions of conulariid midline anatomy recognized in the present study (all photos taken with SEM, figure 6 in backscattered electron mode).

Fig. 1. *Grooved midline with seriated carina* (GSC); part of a series of very low ridges (arrows) along the crest of the inner surface of a midline of *Archaeoconularia membranacea* Sinclair; BMS E10791; Middle Silurian; New York, × 20.

Figs 2–4. *Paired carinae* (PC). 2, inner surface of part of a midline of *Metaconularia* sp.; SUI 37414; Middle Ordovician; Iowa, × 25. 3, fragments (arrows) of paired carinae in *Conularina narrawayi* Sinclair; ROM 18905; Middle Ordovician; Quebec, × 80. 4, fragments (arrows) of discontinuous paired carinae in *Paraconularia chesterensis* (Worthen); ISGS/ISM 2489; Lower Mississippian; Illinois, × 20.

Fig. 5. *Paired thickenings* (PT); transverse section through a pair of midline thickenings (arrows) of *Conularina triangulata* (Raymond); GSC 94788; Middle Ordovician; Quebec, × 80.

Fig. 6. *Low bifid carina* (LBC); inner surface of part of a discontinuously bifid (arrows) midline carina of *Conularia splendida* Billings; UW-BM 73177a; Upper Ordovician; Iowa, × 32.

Figs 7–8. *Single carina, adaperturally bifurcating?* (ABC?). 7, single carina at the broken apical end of one of the faces of the holotype of *Eoconularia amoena* Sinclair; ROM 23297; Middle Ordovician; Quebec, × 300. 8, two carinae (arrows) at the broken apertural end of the widest face of the same specimen, × 130.

PLATE 2

VAN ITEN, conulariids

broader and lower. Because known specimens of *Conularina* are broken well above the apex, it is not yet clear whether the thickenings continue as a discrete pair throughout their length or merge adapically to form a single thickening.

As noted in the preceding section, the corners of *Conularina* are also thickened. In all specimens here examined, the corner thickenings are from two to three times higher than those at the midlines (Text-fig. 3E).

Low bifid carina (LBC) (Pl. 2, fig. 6). This condition was detected in specimens of *Conularia splendida* Billings from the Maquoketa Formation (Upper Ordovician) of northeast Iowa, USA. Midlines of these specimens exhibit a low, broadly rounded or carinate ridge, portions of which are often adaxially bifid. Although this is similar to paired midline carinae, the paired crests of low bifid carinae are parts of a single thickening situated on the midline proper, rather than a pair of separate thickenings straddling the midline.

Single carina, adaperturally bifurcating? (ABC?) (Pl 2, figs 7–8). The existence of this condition, previously detected in certain circoconulariids (Bischoff 1978; see also below), is suggested by inspection of the holotype and only known specimen of *Eoconularia amoena* Sinclair. At this specimen's apical end, now broken, the narrowest face (the specimen exhibits a strongly trapezoidal transverse cross section; see Text-fig. 3F) exhibits a low carina, visible in cross-section (Pl. 2, fig. 7) and indicated on the test surface by a band of strong pigmentation extending along part of the midline. At the opposite end, the widest face exhibits fragments of a pair of carinae, one on either side of the midline proper (Pl. 2, fig. 8). Due to incomplete preservation, it is not possible to determine whether the features detected at the two ends of the specimen are sections through a carina that bifurcates adaperturally, or, for instance, sections through a carina that is discontinuously paired or bifid.

As noted in the preceding section, the corners of *Eoconularia* are strongly carinate. In *E. amoena*, the corner carinae are about three times higher and two times wider than the midline carinae (Text-fig. 3F).

Paired seriated carinae (PSC) (Pl. 1, fig. 6). This condition characterizes specimens of *Climacoconus* collected from Middle and Upper Ordovician strata of the Upper Mississippi Valley, USA and assigned by Sinclair (1948) to one of three species (*C. clermontanus*, *C. concinnus*, and *C. mollis*; see Appendix), all unpublished. The midlines of these specimens are flanked by two files of discrete, closely-spaced ridges. Each ridge is expanded at its ends, making it more or less I-shaped, and extends across a single interspace (the region between the crests of two adjacent transverse ribs). In most specimens, the ridges are strongly pigmented. Members of a pair of files gradually diverge towards the aperture, and the files apparently originate well above the apex. Test material between the two files is thickened. In all four pairs of files, the height and width of the ridges gradually increase towards the aperture.

Corners of the aforementioned *Climacoconus* are sites of a narrow carina. This carina is up to about four times higher than the seriated midline carinae (Text-fig. 3G). As indicated above, a corner carina in at least one fragmentary specimen (GSC 94786a; Pl. 1, fig. 3) shows evidence of seriation. In addition to being higher than segments of paired midline carinae in more complete specimens of the same species, the two preserved corner segments in this specimen were originally several times longer than the midline ridges.

High bifid carina (Text-fig. 4). This condition was discovered by Wiman (1895) in a specimen of *Eoconularia loculata* (Wiman) from the Middle Silurian of Norway (see also Sinclair 1944). Wiman's (1895) three transverse sections (Text-fig. 4A) through this specimen reveal four high carinae whose adaxial portion is strongly bifid. The non-bifid portion of each carina extends about one-third of the way to the centre of the test cavity. From the branching point, the two arms diverge at a high angle and then bend abruptly toward the face. The ends of the arms apparently were free.
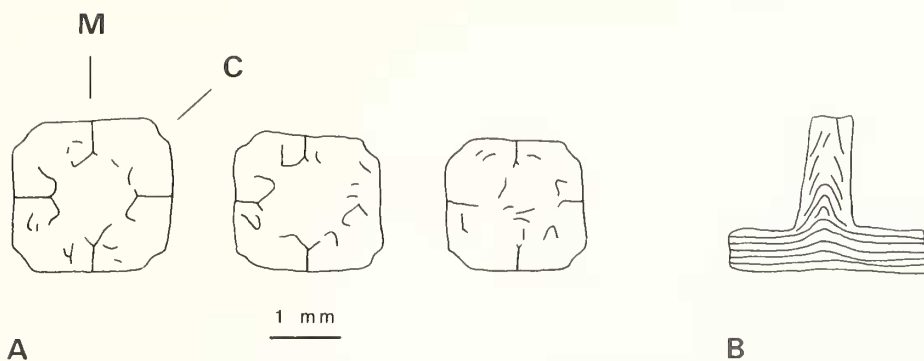
TEXT-FIG. 4. Wiman's (1895, pl. 5, fig. 8–11) line drawings of three transverse sections through a specimen of *Eoconularia loculata* (Wiman), showing: A, the presence of a high, adaxially bifid carina at each of the four midlines; B, inflection and thickening of inner test lamellae in the base of one of the carinae.
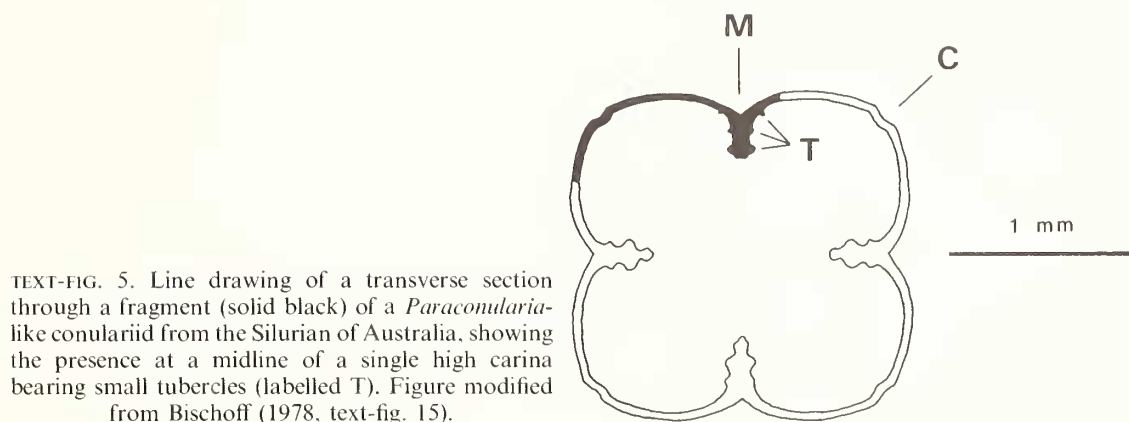
TEXT-FIG. 5. Line drawing of a transverse section through a fragment (solid black) of a *Paraconularia*-like conulariid from the Silurian of Australia, showing the presence at a midline of a single high carina bearing small tubercles (labelled T). Figure modified from Bischoff (1978, text-fig. 15).

Babcock and Feldmann (1986*b*) proposed that these features are not carinae, but taphonomic artefacts possibly caused by differential staining of the rock matrix. Although Wiman's (1895) specimen is currently missing (Babcock and Feldmann 1986*a*), his illustration of the base of one of the midline structures (Text-fig. 4B) clearly shows that it consists of locally inflected and thickened test lamellae, similar to lamellae in carinae observed in other conulariids. Moreover, the midlines were marked by accentuated pigmentation (Wiman 1895, pl. 5, figs 6–7), a feature usually associated with an internal carina. Under these circumstances, and given the indisputable presence of a low bifid carina at midlines of *Conularia splendida* Billings (Pl. 2, fig. 6), it seems wisest to accept Wiman's (1895) characterization of *E. loculata* midlines as accurate.

High tuberculate carina (Text-fig. 5). This condition was detected by Bischoff (1978) in specimens of a *Paraconularia*-like conulariid from the Silurian of Australia. Midlines of this conulariid are marked by a strong, angular sulcus that is associated internally with a single carina that extends about two-fifths of the way to the centre of the test cavity. This carina differs from those discussed above in being covered by small, broadly conical tubercles. The tubercles, arranged on the carina's two flanks, range from about 0·02 to 0·13 mm wide (as measured at their base) and 0·03 to 0·17 mm high (Bischoff 1978).

MIDLINE CONDITIONS OF CIRCOCONULARIIDS

Circoconulariids are represented by abundant but fragmentary material from Silurian and Devonian strata of south-central Australia (Bischoff 1978). Except for their steeply conical (as opposed to steeply pyramidal) shape, circoconulariids are similar to conulariids, consisting of an apatitic, finely lamellar test that is crossed by numerous low, smooth or tubercle-bearing transverse ridges (ribs). In some species, the transverse ribs arch towards the aperture, in such a way as to define eight longitudinal tracts spaced around the test at 45° intervals. Four of these tracts, spaced at 90° intervals, are defined by the summits of segments arching toward the aperture and are interpreted (Bischoff 1978) as homologous to conulariid midlines.

Bischoff (1978) documented five types of internal structures at circoconulariid midlines. Two of these, termed septal ridge and paired septal ridges, are extremely similar, respectively, to single and paired midline carinae of conulariids such as *Paraconularia* and *Metaconularia*. Of the remaining three types of midline structures, two appear to be unique to circoconulariids. The one type that may not be unique to circoconulariids, termed an adaperturally bifurcating low septum, consists of a low carina that splits adaperturally, forming two short branches that diverge at 15–30°. The flanks of this carina (including both single and forked portions) may be smooth or covered by small tubercles, similar to tubercles on the flanks of the midline carina of the *Paraconularia*-like conulariid described above. In some specimens, the midlines show multiple bifurcating septa, arranged in series and with the adapical end of each member of a series situated immediately above the adapertural end of the member below it.

Among the two uniquely circoconulariid midline structures, one structure, similar to multiple bifurcating septa, consists of a series of low, stout, V-shaped ridges, called funnel-shaped septa, that point towards the apex. Individual ridges exhibit a small hole in their adapical end, apparently providing continuous communication between the triangular regions bounded by the two arms of the ridges.

The second uniquely circoconulariid midline structure, termed a septal apparatus, consists of four massive septa that join at the centre of the test cavity, forming a single continuous unit. The sides of each septum exhibit a single longitudinal row of pustules or a coarsely pustulose longitudinal ridge.

SUMMARY OF CONULARIID CORNER AND MIDLINE ANATOMY

Corners and/or midlines of some or all species of at least ten of the twenty-one currently recognized conulariid genera are sites of localized inflection and thickening of inner test lamellae. Internal structures at corners and midlines of most conulariids are smooth; however, the carina at midlines of at least one Australian conulariid, similar to *Paraconularia*, is covered by small tubercles.

Internal midline structures of some or all species of at least six conulariid genera – *Climacoconus*, *Conularia*, *Conularina*, *Eoconularia*, *Metaconularia*, and *Paraconularia* – are paired or bifid. Midlines of *Eoconularia loculata* (Wiman) exhibit an unusually high carina whose cross-sectional geometry is more or less Y-shaped, and midlines of *Eoconularia amoena* Sinclair exhibit features suggesting the presence of a single carina that bifurcates adaperturally.

Corners and midlines of some or all species of five genera – *Archaeoconularia*, *Climacoconus*, *Conularina*, *Eoconularia*, and *Paraconularia* – are both thickened. Except in *Paraconularia crustula* (White), internal corner structures of all such taxa here examined are wider and/or higher than associated midline structures.

Some species of at least two genera – *Archaeoconularia* and *Climacoconus* – exhibit internal corner and/or midline thickenings that are seriated. In *Climacoconus*, where seriation was detected both in midline and corner structures, members of observed corner series are longer and higher than members of observed midline series.

Conulariid midline structures show a number of similarities to midline structures of circoconulariids. Midline structures of both groups represent localized, tetramerally-arranged

inflections of inner test lamellae, and may be smooth or covered by small tubercles. Two types of midline structures, namely single and paired carinae, occur in members of both groups, and a third type, namely a single carina that bifurcates adaperturally, may also be present in both groups.

Together with several other similarities in test anatomy (Bischoff 1978), the similarities outlined above are uniquely shared by conulariids and circoconulariids, and corroborate Bischoff's (1978) contention that these two groups are closely related. For this reason, observed conditions of circoconulariid midlines are regarded here as having a bearing on the interpretation of conulariid anatomy.

SCYPHOZOAN PERRADIAL AND INTERRADIAL ANATOMY

Scyphozoan septa

Except in medusae of the Orders Rhizostomatida and Semaeostomatida, the enteron of all scyphozoans is normally subdivided by four radially disposed, longitudinal septa (Hyman 1940). Abnormal individuals may produce two, three, five, or six septa (Hyman 1940; Berrill 1963).
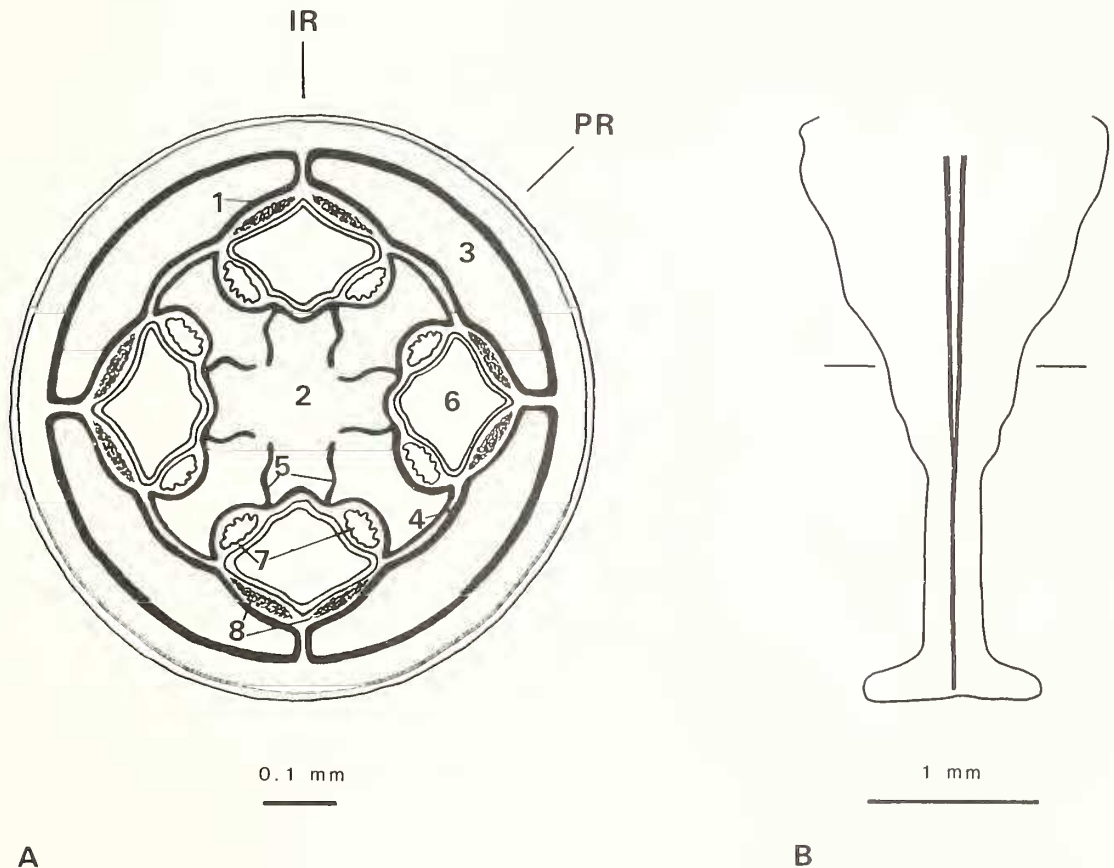

TEXT-FIG. 6. *Craterolophus tethys* Clark, a stauromedusan scyphozoan. A, transverse section near the middle of the polyp. Number symbols indicate the following anatomical features: 1, septum; 2, central stomach; 3, gastric pouch; 4, claustrum; 5, phacellae; 6, peristomial funnel; 7, gonads; 8, retractor muscle. IR and PR stand for interradius and perradius, respectively. B, profile of one of the septal retractor muscles, showing splitting of the muscle to form two strands diverging towards the aperture. Both drawings modified from Gross (1900, pl. 23, fig. 3, pl. 24, fig. 14).

Details of the anatomy of scyphozoan septa have been reviewed by Hyman (1940). Summarizing the main points, each septum is penetrated adorally by a deep, ectoderm-lined, funnel-shaped invagination, the peristomial funnel, that causes the septum to bulge laterally (Text-fig. 6A). In some members of the order Stauromedusida (a group of exclusively sessile scyphozoans), each of the two sides of the septum exhibits a sheet-like longitudinal outgrowth, called a claustrum, that is fused along most of its length with a claustrum of the laterally adjacent septum. The septum's free or adaxial edge exhibits two symmetrically arranged, longitudinal rows, or phacellae, of nematocyst-bearing gastric filaments. Nearer the septum's fixed, or abaxial, edge is a pair of longitudinal, entodermal gonads. Situated still closer to the septum's abaxial edge is a longitudinal retractor muscle, derived from the ectoderm. In most scyphozoans, apparently, the retractor muscle consists of a single tissue bundle; however, in some species of the stauromedusan genera *Craterolophus* Clark and *Lucernaria* Müller, the septal muscle bifurcates adorally (Antipa 1892; Gross 1900; Berrill 1962). In *Lucernaria walteri* Antipa, for example, the muscle splits near the animal's oral end, and the two branches diverge at roughly 20° (Antipa 1892, pl. 17, fig. 1; see also Hyman 1940, fig. 165A); in *Craterolophus tethys* Clarke, the muscle splits nearer the basal end, and the branches diverge at about 2° (Text-fig. 6B).

Coronatid thecal structures

Polyps of the order Coronatida are sheathed in a steeply conical, non-mineralized theca that in some species exhibits internal structures at the interradii and perradii (e.g. Werner 1966a, 1966b, 1967, 1970, 1974, 1979, 1983; Chapman and Werner 1972). The theca is built of numerous, extremely thin (12 nanometres), chitinous lamellae that generally parallel the outer surface of the theca and are grouped in two layers: a thin, outer layer crossed by fine, closely-spaced transverse and longitudinal corrugations; and a thicker, non-corrugated, inner layer. The outer, corrugated layer ranges from about 2 to 4 μm thick and is secreted by soft tissues overlapping the theca's apertural margin. Growth of the outer layer evidently involves extension of the apertural edge of existing lamellae. The inner layer, locally almost 20 μm thick, is secreted by ectoderm of the side of the calyx, which accretes whole lamellae to the theca's inner surface.

In species exhibiting internal thecal structures (Text-fig. 7), the perradii and interradii are sites of a single file or series of discrete, thorn-like longitudinal invaginations of the theca's inner layer. These invaginations, here designated internal thecal projections, are also arranged in whorls, with each whorl consisting of a set of four perradial and four interradial projections. Projections at the
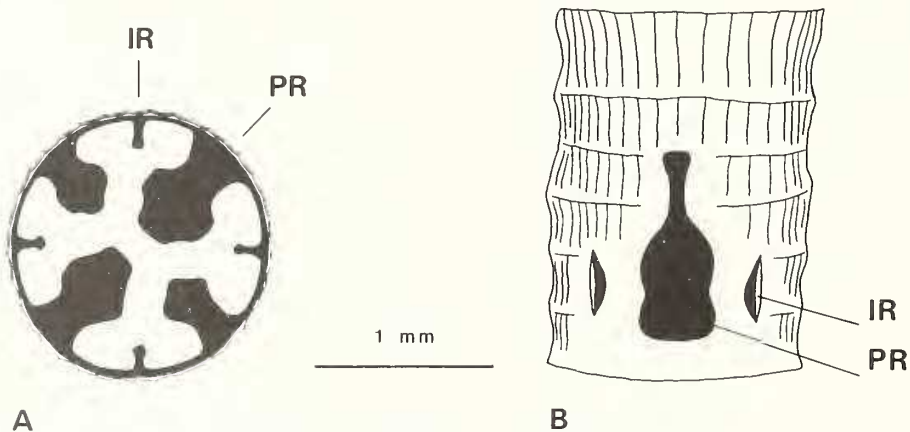
TEXT-FIG. 7. Drawings of internal thecal projections at the perradii (PR) and interradii (IR) of the coronatid scyphozoan *Stephanoscyphus planulophorus* Werner. Drawings modified from Werner (1967, fig. 6b). A, transverse section through a single whorl. B, side view of one member each of a perradial and two interradial files.

perradii are consistently larger (longer, wider, higher) than projections at the interradii, with the perradial projections often extending over half-way to the theca's longitudinal axis. In most species, both sets of projections are smooth; in other species, however, the perradial projections exhibit small tubercles.

COMPARISONS OF SCYPHOZOANS AND CONULARIIDS

The hypothesis that conulariid midlines were sites of a gastric septum, homologous to the gastric septa of scyphozoans, was originally based in large part on comparisons of high, adaxially bifid midline carinae of *Eoconularia loculata* (Wiman) with claustra-bearing septa of stauromedusans such as *Craterolophus tethys* (Kiderlen 1937; Van Iten 1991). As shown in Text-figure 1, both sets of structures are identical in number and arrangement, and show similarities in size (both absolute and relative to the body, or test, cavity) and cross-sectional form. As indicated by previous discussions of other higher taxa (e.g. Jollie 1962; Jones 1985; Barnes 1987), no currently known non-scyphozoan group exhibits soft-part or test structures that more closely resemble *E. loculata* midline carinae than do stauromedusan septa. Coupled with microstructural evidence indicating that the conulariid test was an ectodermal derivative whose growth involved centripetal accretion of whole lamellae (e.g. Bischoff 1978; Van Iten 1991), this suggests that high, adaxially bifid midline carinae, while not directly homologous to stauromedusan septa, were covered in life by soft tissue structures that were homologous to stauromedusan septa.

Midline carinae of other conulariids also exhibit interesting similarities to stauromedusan septa. As noted above in connection with details of septal anatomy, the septal muscle of some stauromedusans consists of a single tissue bundle, while in other stauromedusans the muscle bifurcates adorally. Similarly, conulariids whose midlines are internally carinate exhibit either a single carina, a pair of carinae, or possibly, a single carina that bifurcates adaperturally. Paired midline carinae of relatively small conulariids (e.g. *Conularina narrawayi* Sinclair; Pl. 2, fig. 3) are similar in spacing and angle of divergence to the paired muscle strands of the bifurcate retractor muscle of *Craterolophus tethys*. The geometry of bifurcate midline carinae of the circoconulariid *Garraconularia* Bischoff is similar to the geometry of the retractor muscle of *Lucernaria walteri*, a species in which the paired strands of the muscle's bifurcate portion diverge more rapidly than in *Craterolophus tethys*.

Given that the conulariid (and circoconulariid) test and the scyphozoan septal muscle are both ectodermal derivatives, it seems reasonable to infer that similarities between internal midline structures of conulariid tests and the scyphozoan retractor muscle are indicative of similarity at a more general level of comparison. While test structures at conulariid midlines are not directly homologous to the scyphozoan septal muscle, similarities between these two features could be interpreted as additional evidence that the organization of soft tissues located at conulariid midlines and scyphozoan interradii was fundamentally similar. More specifically, and as proposed earlier by Bischoff (1978), these similarities suggest that the presence of single, paired, or adaperturally bifurcating midline carinae in conulariids (and circoconulariids) reflects the former presence of a septal retractor muscle that could be either single, paired, or adorally bifurcate.

Similarities between internal test structures at conulariid corners and midlines and internal thecal projections at the perradii and interradii, respectively, of coronatid scyphozoans are also important. Both sets of structures consist of tetramerally arranged, longitudinally elongate inflections of inner lamellae, and may be smooth or covered by small tubercles. Just as coronatid perradial projections are consistently larger (higher, broader, longer) than projections at the interradii, in nearly all conulariids whose corners and midlines are both carinate, internal structures at the corners, interpreted as perradial in position, are broader and/or higher than internal structures at the midlines. (The one species here examined where this size relationship is sometimes not observed, *Paraconularia crustula* (White), is substantially younger geologically than other taxa having carinate corners and midlines (see Appendix), and thus it is possible that departure from the more commonly observed condition represents a relatively derived condition.) Internal test structures of

Archaeoconularia membranacea (Ringueberg) and at least two species of *Climacoconus* are seriated. Although seriation in *A. membranacea* is apparent at midlines only, at least one *Climacoconus* species (Sinclair's (1948) unpublished *C. concinnus*; GSC 94786) shows evidence of seriation at both midlines and corners. Segments of seriated corner and midline carinae in *Climacoconus* are organized in isolatitudinal groups or whorls (currently available specimens of *A. membranacea* are too incomplete to determine if their internal midline structures are arranged in whorls), and, like coronatid perradial projections, segments of seriated *Climacoconus* corner structures are several times longer and higher than segments of seriated midline structures.

The presence of internal test or thecal structures having the characteristics summarized above is a feature uniquely shared by certain conulariids and coronatid scyphozoans, and thus tends to corroborate the hypothesis that the organization of soft tissues at conulariid midlines and scyphozoan interradii was fundamentally similar. In addition, similarities between internal structures of conulariid tests and coronatid thecae raise the possibility, already suggested by Chapman (1966) and Werner (1966a), that the most recent common ancestor of conulariids and coronatids was a thecate animal having internal thecal projections at the perradii and interradii. Interestingly, conulariids having internal carinae, either continuous or seriated, at both corners and midlines (e.g. *Archaeoconularia fecunda* (Barrande), *Climacoconus*, *Conularina*, and *Eoconularia forensis* Sinclair), are among the earliest (and thus, possibly, least differentiated from a common conulariid/coronatid ancestor) conulariids known.

Finally, just as aberrant scyphozoans produce two, three, five, or six septa, *Conularina triangulata* (Raymond) has only three faces (and hence three midlines), and Babcock *et al*. (1987b) documented a specimen of *Paraconularia missouriensis* (Swallow) with six faces. The only other metazoans resembling conulariids and known to exhibit this array of alternate symmetries are hydrozoan cnidarians (which, for example, show variation in the number of primary branches in the medusa's radial canal system; Werner 1973).

To summarize, conulariid corners and midlines exhibit numerous similarities to anatomical structures located, respectively, at the scyphozoan perradii and interradii. Except for similarities in symmetry patterns (which are also shared with hydrozoan cnidarians), all of the similarities outlined above are uniquely shared by conulariids and scyphozoans, and there is no evidence of greater similarity between conulariid corners and midlines and test or soft-part structures of any non-scyphozoan group. The relatively complex character of similarities between conulariid corners and midlines and scyphozoan perradial and interradial anatomy makes it difficult to dismiss these similarities as superficial or due to convergence. Rather, these similarities suggest that conulariid midlines were sites of a gastric septum, homologous to the gastric septa of scyphozoans. (It should be noted here that Babcock and Feldmann (1986a, 1986b) proposed that the tendency of many conulariids to be distinctly rectangular in transverse cross-section indicates that conulariids were 'bilaterally symmetrical' organisms that exhibited a higher level of anatomical organization than that shown by scyphozoans or other cnidarians; however, 'bilateral (biradial) symmetry' is exhibited by structural elements (e.g. whorls of internal thecal projections) of coronatid thecae (Text-fig. 7A), and thus its occurrence among conulariids in no way weakens anatomical interpretations advocated in this study.)

IMPLICATIONS FOR CONULARIID AFFINITIES

Proponents of the hypothesis that conulariid midlines were sites of a gastric septum interpret conulariids as extinct members of the Phylum Cnidaria, a monophyletic taxon whose extant members are generally thought to include the Classes Anthozoa, Hydrozoa, and Scyphozoa (a number of authors interpret cubozoans, traditionally regarded as a group within Scyphozoa, as a fourth cnidarian class; e.g. Werner 1973; Petersen 1979; Möhn 1984; Brusca and Brusca 1990). Relationships among these three classes (and conulariids) have been subject to widely divergent interpretations (e.g. Jägersten 1955, 1959; Hill and Wells 1956; Marcus 1958; Hadzi 1958, 1963; Hand 1959; Uchida 1963; Thiel 1966; Glaessner 1971, 1984; Werner 1973; Salvini-Plawen 1978;
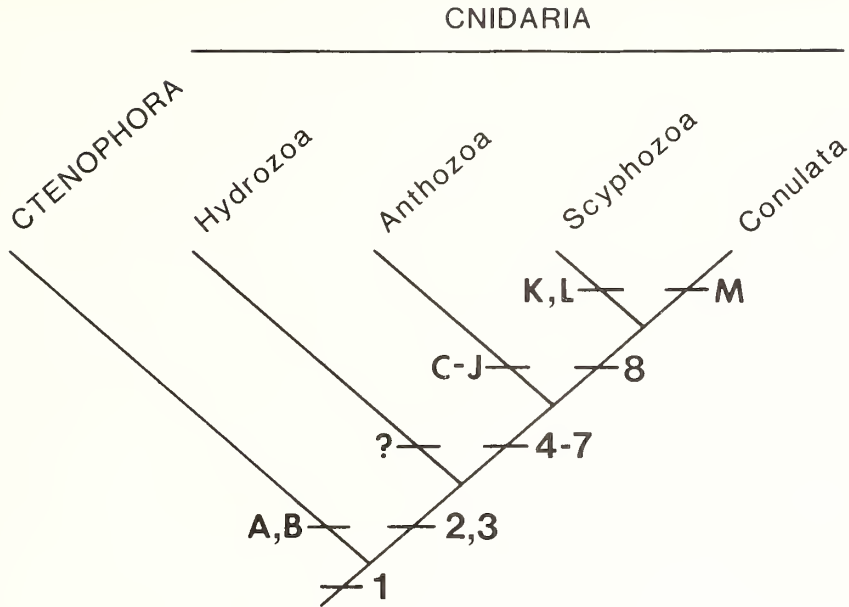
CNIDARIA

TEXT-FIG. 8. Cladogram summarizing one interpretation of phylogenetic relationships among conulariids and extant cnidarians. The Phylum Ctenophora is interpreted as the nearest living relative of Cnidaria. Synapomorphies (numbered) are as follows: 1, diploblastic, tentacle-bearing medusa with non-septate digestive cavity having four radially disposed primary branches that bear the gonads; 2, cnidae; 3, planula larva; 4, gastric septa; 5, cnidae-bearing gastric filaments; 6, sex cells ripening in entoderm; 7, mesenchyme cellular; 8, four septa. Autapomorphies (lettered) are as follows (C–J taken from Brusca and Brusca 1990, fig. 43A); A, cydippid larva; B, comb rows; C, loss of medusa; D, hexaradial and octaradial symmetry; E, actinopharynx; F, siphonoglyph; G, loss of cnidal operculum; H, loss of cnidocil; I, cnidae with tripartite flaps; J, cnidae with special ciliary cones; K, rhopalium; L, strobilation; M, apatitic theca. No autapomorphies are shown for Hydrozoa, interpreted by Brusca and Brusca (1990) as a paraphyletic taxon.

Grasshoff 1984; Möhn 1984; Brusca and Brusca 1990; Willmer 1990), and extended analysis of this problem lies beyond the scope of the present discussion. Nevertheless, the presence of four septa in conulariids and scyphozoans may mean that these two groups are more closely related to each other than either group is to anthozoans, which have a greater number of septa, or to hydrozoans, which lack septa. At this point there appear to be no similarities between conulariids and anthozoans or hydrozoans that are not also shared with scyphozoans, and thus there are no similarities that conflict with the hypothesis that conulariids and scyphozoans are nearest relatives. This hypothesis is outlined in Text-figure 8, which also summarizes the more general hypothesis of relationships, favoured by a number of previous authors (e.g. Hyman 1940; Hill and Wells 1956; Hand 1959; Uchida 1963; Brusca and Brusca 1990), that septate cnidarians form a monophyletic group within Cnidaria that excludes hydrozoans.

This and other proposed hypotheses of relationships among taxa within Cnidaria (e.g. medusa-bearing cnidarians form a monophyletic group within Cnidaria that excludes anthozoans; Werner 1973) are in serious need of further testing. Thus far work on this problem has centred largely on analysis of gross anatomical characters such as the presence or absence of septa and the structure of the cnidae (Text-fig. 8). However, additional characters, including the structure of mitochondrial DNA (e.g. Warrior and Gall 1985) and the ultrastructure of sperm (e.g. Hinsch 1974; Schmidt and Hölken 1980), are being explored in some detail, and it will be important to extend this research to cover possible close relatives of Cnidaria such as the Phyla Ctenophora and Platyhelminthes (e.g.

Bayer and Owre 1968; Harbison 1985), one or both of which may be sufficiently similar to Cnidaria to serve as outgroups for cladistic parsimony analysis of relationships within that group.

Needless to say, more work is also needed on conulariids (and circoconulariids), particularly on details of their life history and soft part anatomy. Some of this information may be contained in material from the Hunsrück Slate (Lower Devonian, Germany), which has yielded several pyritized specimens of *Conularia* containing probable relic soft parts (Steul 1984; Van Iten 1989, 1991).

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APPENDIX

Conulariids examined in the present study. Letter symbols in parentheses next to a species name indicate conditions of that species' corners and midlines, respectively, and are as follows: NS, non-sulcate; SG, simple groove, MFG, mesially folded groove; CG, carinate groove; S, simple; OF, outwardly folded; SC, single carina; GSC, groove with seriated carina; PC, paired carinae; PT, paired thickenings; LBC, low bifid carina; ABC?, single carina, adaperturally bifurcating?; PSC, paired seriated carinae. N = number of specimens of a given species currently available and/or observed to exhibit conditions listed next to that species' name. Institutions housing examined specimens are as follows: AC, Augustana College, Rock Island, Illinois; AMNH, American Museum of Natural History, New York; BMS, Buffalo Museum of Science, Buffalo; BMNH, British Museum (Natural History), London; BMUW, Burke Museum, University of Washington, Seattle; CM, Carnegie Museum, Pittsburgh; FMNH, Field Museum of Natural History, Chicago; GSC, Geological Survey of Canada, Ottawa; ISGS/ISM, Illinois State Geological Survey/Illinois State Museum, Champaign/Urbana; 1U, Indiana University, Bloomington; LACM, Los Angeles County Museum, Los Angeles; MCZ, Museum of Comparative Zoology, Harvard University; NYSM, New York State Museum, Albany; PMNH, Peabody Museum of Natural History, Yale University; PRM, Peter Redpath Museum, Montreal; ROM, Royal Ontario Museum, Toronto; SUI, State University of Iowa, Iowa City; UMMP, University of Michigan Museum of Paleontology, Ann Arbor; UMMP*, University of Montana Museum of Paleontology, Missoula; UI, University of Illinois, Champaign–Urbana; UMPC, University of Minnesota, Minneapolis; USNM, United States National Museum, Washington.

Species	Horizon/Age	Locality	Repository	N
Anaconularia				
A. *anomala* (Barrande) (NS, ?)	Drabov Qtzite (M. Ord.)	Bohemia	MCZ	≈ 760
Archaeoconularia				
A. *membranacea* Sinclair (CG, GSC)	Rochester Fm. (M. Sil.)	New York	BMS E10791, E10793	2
A. *mirifica* (Reed) (SG, SC)	Drummock Gp (U. Ord.)	Scotland	GSC 87280*a–d*	4
Calloconularia				
C. *strimplei* Sinclair (CG, SC)	Ochilate Gp (Penn.)	Oklahoma	FMNH PE143*a*	1
Climacoconus				
C. *batteryensis* (Billings) (?, SC)	Vaurél Fm. (U. Ord.)	Quebec	GSC 29594; PMNH 10367	2
C. *bromidus* Sinclair (CG, SC)	Viola Fm. (M. Ord.)	Oklahoma	USNM	3

APPENDIX (*cont.*)

Species	Horizon/Age	Locality	Repository	N
C. bureaui Sinclair (SG, S)	Trenton Gp	Quebec	GSC 17852	1
C. quadratus (Walcott) (CG, S)	Tetreauville Fm. (M. Ord.)	Quebec	GSC 17710–17712	3
C. cf. *quadratus* (CG, S)	Maquoketa Fm. (U. Ord.)	Iowa	SUI 61534	1
C. rallus Sinclair (CG, S)	Laval Fm. (M. Ord.)	Quebec	GSC 17713	1
C. sp. 1 (CG, PSC)	Platteville Fm. (M. Ord.)	Minnesota	GSC 94785*a–g*	7
C. sp. 2 (CG, PSC)	Platteville Fm. (M. Ord.)	Minnesota	GSC 94786*a–b*; UMMP 20650	4
C. sp. 3 (CG, PSC)	Maquoketa Fm. (U. Ord.)	Iowa	GSC 94787; SUI 61531	2
C. urbanis Sinclair (CG, S)	Quebec City Fm. (M. Ord.)	Quebec	GSC 17853	1
Conularia				
C. albertensis Reed (?CG, SC)	Devonian	Bolivia	USNM 409813–409814	2
C. delphiensis (Maroney and Orr) (SG, S)	New Albany Sh. (U. Dev.)	Indiana	UMMP 66085	≈ 50
C. formosa Miller and Dyer (SG, S)	Stonington Fm. (U. Ord.)	Michigan	UMMP 30369	1
C. milwaukeensis Cleland (CG, S)	M. Dev.	Wisconsin	UMMP 814	1
C. multicostata Meek and Worthen (SG, S)	Cuyahoga Sh. (L. Miss.)	Ohio	AC I-4160, I-4164; UMMP 804	3
C. cf. *splendida* Billings (SG, LBC)	Maquoketa Fm. (U. Ord.)	Iowa	SUI 61521–61523; BMUW 73177	7
C. sp. (SC, S)	Cedar Valley Fm. (M. Dev.)	Iowa	SUI 62673–62677, 62683–62693	14
C. subcarbonaria Meek and Worthen (SG, S)	U. Dev.-L. Miss.	USA	FMNH; IUPC; UI	10
C. trentonensis Hall (SG, S)	M.-U. Ord.	USA, Canada	GSC; NYSM; ROM; SUI; UMMP	≈ 100
Conularina				
C. irrasa Sinclair (CG, PT)	Laval Fm. (M. Ord.)	Quebec	GSC 17714	1
C. narrawayi Sinclair (CG, PC)	Laval Fm. (M. Ord.)	Quebec	ROM 18905	1
C. raymondii Sinclair (CG, PT)	Laval Fm. (M. Ord.)	Quebec	GSC 17715	1
C. triangulata (Raymond) (CG, PT)	Laval/Valcour Fms (M. Ord.)	Quebec, New York	CM 2099, 2100, 17714; GSC 17716–17717, 94788–94789	6
Ctenoconularia				
C. obex Sinclair (SG, S)	Platteville Fm. (M. Ord.)	Minnesota	GSC 87193; UMPC 6608	3
C. sp. (SG, S)	Sherman Falls Fm. (M. Ord.)	Ontario	GSC 94784	1

APPENDIX (*cont.*)

Species	Horizon/Age	Locality	Repository	N
Eoconularia				
E. *amoena* Sinclair (CG, ABC?)	Sherman Falls Fm. (M. Ord.)	Quebec	ROM 23297	1
E. *forensis* Sinclair (CG, SC)	Quebec City Fm. (M. Ord.)	Quebec	GSC 1712–1713, 87201	3
Glyptoconularia				
G. *gracilis* (Hall) (CG, ?)	Tetreauville Fm., Trenton Gp. (M. Ord.)	Quebec, New York	AMNH 789; GSC 94782–94783	3
Metaconularia				
M. *aspersa* (Slater) (SG, PC)	Ludlow Sh. (Sil.)	England	BMNH G4603, G5373	2
M. *calderi* Sinclair (SG, PC)	Cobourg/Ottawa Fms (M. Ord.)	Ontario	GSC 9794–9795	2
M. *delicatula* (Savage) (?, PC)	Maquoketa Gp (U. Ord.)	Illinois	UI X-614	1
M. *gibraltarensis* (SG, PC)	Manitoulin Fm. (L. Sil.)	Ontario, Michigan	ROM 7537; UMMP 66023	2
M. cf. *heymani* (Foerste) (SG, PC)	Maquoketa Fm.	Iowa	SUI 62672	1
M. *manni* (Roy) (?, PC)	Lecthaylus Sh. (Sil.)	Illinois	FMNH PE6252–6256, PE10132, PE23674–23975, FMNH unnumbered	13
M. *papillata* (Hall) (SG, PC)	Trenton Gp (M. Ord.)	New York	AMNH 790; MCZ 27809	2
M. sp. (SG, PC)	Dubuque Fm. (U. Ord.)	Iowa	SUI 37414, 62678–62679	3
M. *ulrichi* Foerste (SG, PC)	Platteville Fm. (M. Ord.)	Wisconsin	USNM 43087	1
Notoconularia				
N. *laevigata* (Morris) (MFG, S)	Permian	New South Wales	UMMP 9299	1
Paraconularia				
P. *arctica* Babcock (?, SC)	Permian	Canada	GSC 90696	1
?P. *byblis* (White) (SG, S)	English River Fm. (U. Dev.)	Iowa	UMMP 259, 2167	2
P. *chesterensis* (Worthen) (SG, PC)	U. Miss.	USA	ISGS/ISM 2489; LACM 9364*a*; UMMP 23955	3
P. *crustula* (White) (CG, SC)	Pennsylvanian	USA	UMMP 66024*a–n*; ISGS/ISM 4018, 7865	18
P. *missouriensis* (Swallow) (SG, S)	L. Miss.	USA	FMNH 1125, 6627–6628; ISGS 2619; UMMP 26740	5
P. *planicostata* (Dawson) (SG, SC)	Windsor Gp (Miss.)	Nova Scotia	ROM 29823	14
P. *subulata* (Hall) (SG, S)	Heath Fm. (L. Miss.)	Montana	CM 34521, 34524, 35000; UMMP* 5613, 5628, 5633	6

APPENDIX (*cont.*)

Species	Horizon/Age	Locality	Repository	N
P. ulrichana (Clarke) (SG, SC)	Devonian	Bolivia	USNM 409842–409843	2
Pseudoconularia *P. mirifica* (Spencer) (SG, OF)	Lockport Fm. (L. Sil.)	Ontario	PRM 1019	1
Reticulaconularia *R. penouili* (Clarke) (SG, S)	Grande Grève Ls. (L. Dev.)	Quebec	NYSM 9412	1